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Space use by Black-tailed Godwits *Limosa limosa limosa* during settlement at a previous or a new nest location

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Capsule Black-tailed Godwits first return to the nest location of the previous year, even when moving to a different nest location later that season.
Aims To examine the use of space by Black-tailed Godwits during the two months before egg-laying to two weeks afterwards.
Methods We compare the spatial distribution of sightings of eventually site-faithful birds with birds that changed nest location, and relate this to the change of the distance to their previous year's and current nest-site in the period until egg-laying. Using a log-likelihood model we establish how the differences in distance to the respective nests change over the course of the season.
Results All birds were observed first near their previous year's nest-site, and remained there for most of the pre-laying period. Birds that subsequently changed nest location made the move only about five days before egg-laying and were more wide-ranging earlier on.
Conclusion The return to the previous nest-site suggests that a decision to move is made only after considerable time investment near the previous nest-site. This indicates that site-faithfulness in Black-tailed Godwits is conditional on experiences after return to the nesting area.

Choosing a good nest location is crucial for successful breeding. Migratory birds, perhaps arguably, are more time- and energy-constrained than resident birds (Farmer & Wiens 1999, Nolet & Klaassen 2005, Drent *et al.* 2006). For them, an early acquisition of a high quality breeding site as soon as possible after arrival on the breeding grounds may be especially important. Site-faithfulness would help birds to settle more rapidly, and several migrant shorebirds indeed show great site-faithfulness (Groen 1993, Jackson 1994, Flynn *et al.* 1999). Nevertheless, the decision to use the previous year's nest location again should be conditional on both the previous experiences (breeding success leading to return to the same place, Oring & Lank 1982) and the conditions encountered after return (Dale *et al.* 2006). For a passerine and a seabird there is evidence that breeding site selection is related to experiences in the previous season (Boulinier *et al.* 1996, Pärt & Doligez 2003).

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The behaviour that precedes the decision of where to breed is called prospecting: it provides a means to gather information about the quality of possible breeding sites, and so-called 'public information' is one source of relevant knowledge (Danchin *et al.* 2004). The quality of a breeding site can be judged by food availability, the absence or presence of nest predators and/or the mere presence or the breeding success of conspecifics, in the latter case certainly assessed in previous seasons (Danchin *et al.* 1998, Ward 2005, Parejo *et al.* 2006).

One component of prospecting would be movements near and far from potential nesting sites. Here we present a study of such movements in Black-tailed Godwits *Limosa limosa limosa* in a grassland area in the northern Netherlands. Mapping of individually colour-marked birds over a two-month period enabled us to document the ranging of individuals that remained either faithful to the nest location of the year before, or actually changed nest-site. While most studies focus on events in previous years influencing the decision of

whether to 'stay or go', we use individual movements before the establishment of a nest location and the start of egg-laying. We capitalized on a situation (perhaps due to early overgrazing by geese, see Discussion) where many godwits decided to change nest location from the one used in the previous year.

STUDY AREA AND METHODS

This study was carried out in the northern part of the Workumerwaard, The Netherlands (52°59′N, 5°24′E), an area of 300 ha that includes extensively managed meadows in a polder, called Binnenwaard, and a grassy marshland area, called Buitenwaard, bordering Lake IJsselmeer (Fig. 1a). The polder is intersected by a road and the different meadows are separated by canals. The polder and the shoreline marshland are separated by a low dyke and a 7 m wide canal. The meadows in the polder are managed according to agricultural nature-management schemes, in which only dung and manure are used to the exclusion of artificial fertilizer, and earliest mowing dates are 8 or 15 June. The shoreline marshland is managed as a nature reserve where the public are not allowed and mowing is limited to the dyke. The reserve is not fertilized, and cows and horses graze there at low density in summer. The study area harbours one of the highest densities of breeding Black-tailed Godwits in The Netherlands (Teunissen & Soldaat 2005). In 2004 and 2005, 123 adult breeding Black-tailed Godwits were captured on the nest and received easily readable individual colour-ring combinations consisting of four rings with four possible colours (white, yellow, red or blue) and a yellow flag (University of Groningen 2008). On the basis of a small blood sample taken from the brachial vein, birds were sexed by molecular methods (Schroeder *et al.* 2008).

From March to May 2006, at least three times per week, both the Binnenwaard and Buitenwaard were searched for godwits and the locations of individually colour-ringed birds were mapped to the nearest 50 m on a grid. Arrival dates were defined as the first day in 2006 that an individual was seen in the study area.

In both 2005 and 2006, nests were searched by local volunteers of the meadow bird conservation group Fûgelwacht Warkum, who reported approximate locations to us. We revisited the nests and determined exact positions with handheld Garmin GPS 12 devices to the nearest 2 m. We used three different methods to link individual birds to their nests. Battery-powered digital video-cameras (Technaxx C-2000) were set up

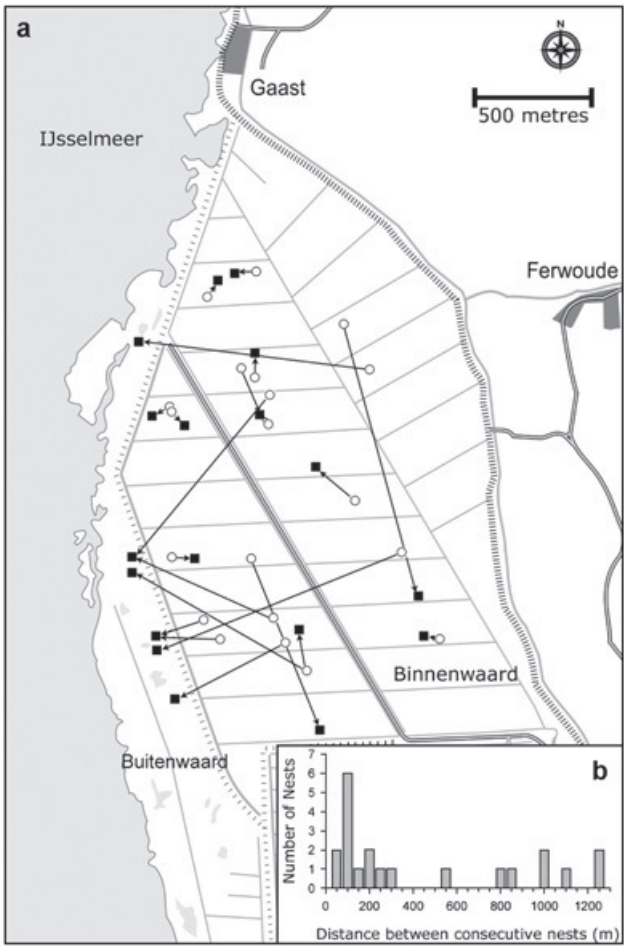

Figure 1. (a) Map of the research area, showing nests of individual Black-tailed Godwits for which nest-sites were known in 2005 (○) and 2006 (■). The lines connect nest-sites of individuals in both years. (b) Distances between nests of the same individuals for 2005 and 2006 in 50 m intervals.

1.5 m away from each nest and left there for 45 minutes. Most breeding birds returned to their nests soon after we left the meadow, and this allowed us to read the colour rings of the bird on the video. In cases where no birds were recorded on the nest, we tried again, up to three times. In the rare cases where no birds would return to a nest with a video camera placed nearby, we tried reading the ring combinations from a hide. We further linked birds to their nest by recapturing adults on the nest. These efforts yielded a total of 21 individual birds for which the nest-site was known in both 2005 and 2006. These were mostly single birds within pairs. There were three pairs in 2006; one pair in 2005 were not together in 2006, and one pair we are certain had remained a pair between the two years, but whether the third pair was also

together in 2005 is unknown. Leaving out either of the two mates in the pair that moved together, to avoid possible pseudoreplication, did not change the outcome of the statistical analyses qualitatively. To ensure the fullest possible presentation of movements, we left them in.

A total of 163 observations were available for these 21 birds. No observations of the period after hatching or loss of the nest were used. Birds were almost never observed after nest loss, which suggests that they left the area quickly. The number of observations per individual varied widely, from 1 to 22 (mean of 8.1 observations per bird ±1.2 se). For an indication of the accuracy of our estimates of arrival times, we calculated a resighting probability by averaging all individual probabilities to resight a bird after they were known to have arrived in the study area. The probability to resight an individual on any single day, when averaged over the whole study period for all birds, was 0.24 (±0.02 se, $n = 20$).

For each observation, we determined the number of days prior to laying the first egg for that individual. For all analyses we then used the number of days from the moment of observation until the start of egg-laying; for example an observation made on day 12 would mean it was made 12 days before the nest of that individual godwit contained an egg for the first time. In our analysis of individual space use, relative to birds' former and future nests, we used only the distances of the individual observations before start of egg-laying to either the former or present nest locations in 2006. We emphasize that not all birds were observed for the same period of time prior to egg-laying, due to individual differences in timing of arrival and the timespan between arrival and the start of egg-laying.

Lay dates were estimated by measuring the degree of buoyancy of the eggs, which is related to the incubation stage (van Paassen *et al.* 1984, Liebezeit *et al.* 2007). We used a correction factor for nests found when they were still incomplete to ensure that in the analysis 'lay date' is the start of egg-laying, and not the start of incubation. Assuming that it took five days to complete a clutch, and that there were four eggs per clutch (Beintema *et al.* 1995), nests found with one, two or three eggs were assumed to be incomplete and the lay date was corrected to one, two or three days prior to finding the nest, respectively. All dates used are April days, where 1 April is day one. Based on Groen (1993), who showed that 80% of Black-tailed Godwits build their nest within 250 m of the nest location in the previous breeding season, *movers* denote birds that either moved more than 250 m away from their former nest-sites or that changed breeding location to the Buitenwaard. *Stayers* are birds that nested in 2006 within 250 m from the nest location in 2005 (Fig. 1b shows the frequency distribution of the distances between consecutive nests).

To establish whether the difference in distance to nests between movers and stayers was statistically significant, the statistical software program MLwiN (Version 2.02, 2005) was used to perform hierarchical linear models (Bryk & Raudenbush 1992). These models take the nested relationship of repeated measures of individuals on different days into account. In our analysis we used two levels: individual and repeated measures. We used the standardized distance to the future nest-site as dependent variable. The standardization was calculated by simply subtracting the mean distance of all observations from the actual distance of each individual observation. This centred the values on a mean of zero. Predictor parameters were removed successively from the full model, starting with the least significant highest interactions. Significance was tested using the increase in deviance, which follows a chi-squared distribution. As predictor variables we used 'days until initiation of the new nest', 'sex' and 'mover–stayer', with stayer as reference. To account for intercorrelation of repeated observations of the same individual, 'individual bird' was added as a random factor into the model.

RESULTS

In 2006, the average arrival date of our focal birds was 25 March (±1.5 days se, first arrival on 12 March); no differences were apparent between the sexes (Student's *t*-test, $t = 0.4283$, df = 19, $P = 0.34$). Returning Black-tailed Godwits were first observed significantly closer to their previous nest location than to their future nest-site (paired *t*-test, $t = 2.66$, df = 20, $P = 0.01$), with 136 m (±48 se) and 415 m (±91 se), respectively, for the 2005 and 2006 nest locations. The average distance to the future nest-site for the whole period was 390 m. Again, there were no differences between the sexes ($t = 0.37$, df = 19, $P = 0.72$). Sex did not show an effect on the distance to the future nest-site in any of the models we tested. Of the 21 birds for which exact nest locations were known in the two years, nine were movers and 12 stayers (Fig. 1). There is no difference in number of observations per bird between the groups (*t*-test, $t = 1.19$, df = 19, $P = 0.25$).

When grouping observations into five-day periods (Fig. 2) it is clear that all birds arrived close to their

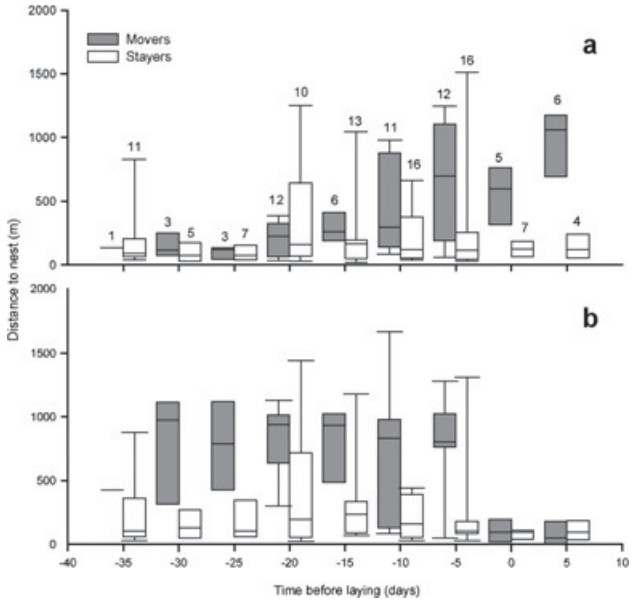

Figure 2. The effect of days until laying on the distance individual Black-tailed Godwits observed from their previous (2005) nest-site (a) and future (2006) nest-site (b) for birds that moved less than 250 m between years (white) and more than 250 m (grey). Indicated are median, 25–75% boxes and 95% confidence intervals. The observations are pooled in five-day periods. Above each box the number of observations in that period is shown. The graph is cut off at five days after the start of incubation, since movers and stayers both stay close to their nest during incubation.

breeding site of the previous year. The movers seemed to start moving away from these sites 15 to 10 days prior to laying (Fig. 2a), but were found close to their new nest-site only around the time of egg-laying (Fig. 2b). In our final model (parameters displayed in Table 1), the interaction of 'days until laying' and 'movers and stayers' was found to be significant, while sex was dropped from the model. This model showed that before nest initiation, the movers were seen further away from their 2006 nest-site (mean 723 m ± 407 se) than stayers (mean 283 m ± 398 se; t = –5.0, df = 161, $P < 0.0001$), and this distance declined with date only for the movers (Fig. 2b). This indicates that the movers ranged over increasingly greater distances from the previous breeding site than the stayers before they settled.

During incubation, the two categories (movers and stayers) did not show significant differences (t = 1.41, df = 10, P = 0.19) in average distance from their actual 2006 nest location (142 m ± 224 se). The average is strongly influenced by a single observation of a bird seen at 1000 m from its nest; without this observation the average distance was 98 m (±19.5 se).

Table 1. Distance to future nest-site in relation to days until laying, and whether individuals moved nest-sites.

	Standardized distance to nest		
Parameter	β (se)	χ^2 (df = 1)	P
Intercept	–0.504 (0.214)	5.527	0.018
Moved	0.5 (0.285)	2.991	0.084
Days from laying	–0.003(0.007)	0.142	0.710
Moved * Days from laying	–0.036 (0.011)	11.019	0.001

The table gives the most parsimonious log-likelihood model (–2 log-likelihood value = 386.163) constructed in MLwiN and showing the effect of moving/staying on the standardized distance to the future nest. In this mixed model individual identity was included as random effect. 'Moved' is a categorical variable to distinguish between birds breeding within 250 m of the previous nest or further than 250 m. 'Days from laying' is the number of days until the start of egg-laying by an individual bird.

DISCUSSION

Upon arrival on the Dutch breeding grounds, Black-tailed Godwits were first observed closer to the breeding site of the previous breeding season than to the site eventually used in the current year, suggesting that their first choice of breeding site was that of the previous year. Birds that were site-faithful remained there, but birds moving to a more distant nest-site did so only about five days before the start of egg-laying. This would be expected given the high nest-site fidelity in Black-tailed Godwits (Groen 1993), but the relatively high frequency of movements in our study needs explanation.

An obvious explanation for the greater distance moved by the movers prior to breeding might be that we did not observe all nesting attempts, and that the nests we observed for the movers were replacement clutches. Although this is possible, the two groups did not differ in arrival date on the breeding grounds (t-test, t = 0.90 df = 19, P = 0.38), nor in the date of clutch initiation (t-test, t = 0.09, df = 19, P = 0.93). Therefore we have no reason to believe that we missed more first clutches in one of the two groups.

It is possible that the old breeding site is used as a meeting place for partners. Black-tailed Godwits are socially monogamous, but pairs often winter far apart, as has been shown for the Icelandic Black-tailed Godwit *Limosa l. islandica* (Gunnarson *et al.* 2004). After arrival on the breeding grounds, there is usually only a brief opportunity for migratory birds to reunite with the partner before the start of breeding

(Choudhury 1995). Therefore, a fixed location to reunite could prevent the need to spend precious time searching for the partner and this would allow for earlier breeding.

After reuniting, the godwits might prospect the suitability of the breeding area, using some sort of cue predicting its future condition. Food availability could be used as a possible cue since timing of breeding is often matched with timing of food availability for chicks (Hochachka 1990, Thomas *et al.* 2001, Dunn 2004). For Black-tailed Godwits insect abundance during chick rearing is an important component of nest-site suitability (Schekkerman & Beintema 2007). Another factor important for nest success of ground-breeding birds is nest predation, which is likely to be related to vegetation structure (Pärt 2001, Whittingham & Evans 2004). The Buitenwaard, where many movers went to breed in 2006, has a different vegetation composition from the abandoned nest-sites on the Binnenwaard. At least in 2006 the Buitenwaard had rougher and higher vegetation in the weeks before egg-laying. This contrasted with the situation on the Binnenwaard, especially in April 2006, which was grazed down to very short swards by Barnacle Geese *Branta leucopsis* (unpubl. data). We suggest that the birds departed from these short swards because nests would have been unconcealed from predators, and the phenology of insect availability may have been late relative to hatching. These movements to the Buitenwaard, however, did not result in higher reproductive success, because a large number of nests on the Buitenwaard were destroyed when the area was flooded during a storm.

An additional explanation for the observed long-distance breeding site changes might be mate change. It is often found that the divorce of bird pairs is not caused by a search for a better mate but rather by the search for a better territory. A number of studies report that it is the females that move, sometimes considerable distances, to a new territory (see references in Black 1996). This change of territory, and of mate, is observed to have negative consequences for reproductive success in the first season after the move to the new territory. Unfortunately, our current sample sizes do not allow further analysis (of the nine movers, six were females, three were males; we observed only one certain divorce). In a year when the quality of the former breeding grounds has apparently deteriorated, we would expect that movers more often divorce to find a better nest-site and that females show the greater dispersal distances. The short time interval between movement and final egg-laying, however, suggests that movements were made by pairs together, rather than involving a switch in mates.

The higher variance in the distance to the nest before incubation shown by the movers (Fig. 2) indicated greater movement. This may be interpreted as prospecting in other areas. When they leave their previous breeding site relatively late to breed elsewhere, the movers might be making the best of a bad situation, as the most favoured territories will already be occupied by other birds. However, Black-tailed Godwits are semi-colonial breeders, who may cue on the presence of others to guide their nest choice and profit from each other by collectively defending nests against predators. This may allow them to move to other sites relatively late during the nesting season without too high a cost.

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